

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

What hummingbirds can tell us about cognition in the wild

Susan D. Healy, University of St. Andrews, St. Andrews, Fife, UK

T. Andrew Hurly, University of Lethbridge, Lethbridge, Alberta, Canada

Here we review around 20 years of experimental data that we have collected during tests of cognitive abilities of free-living, wild rufous hummingbirds *Selasphorus rufus* at their breeding grounds in southwestern Alberta. Because these birds are readily trained to feed from artificial flowers they have proved a useful system for testing cognitive abilities of an animal outside the box wherein animal cognitive abilities are so often tested in the laboratory. And, although these data all come from a single species in a single location, the long-term aim of this work is to make a contribution to our understanding of the evolution of cognitive abilities, by examining the relationship between the ecological demands these birds face and their cognitive abilities. Testing predictions based on our knowledge of their ecology we have found that, while these birds aggressively defend a territory and display to females during the time we train and test them, they can learn and remember the locations of rewarded flowers, what those flowers look like, and when they are likely to contain food. Small-brained though they may be, these 3g hummingbirds appear to have cognitive capabilities that are not only well matched to their ecological demands, they are in at least some instances better (more capacious) than those of animals tested in the laboratory.

Keywords: hummingbird; field research; spatial orientation; timing; choice

Around 15 years have passed since the publication of *Animal Cognition in Nature* (Balda, Pepperberg, & Kamil, 1998). Ironically, this was a volume that did not, in fact, actually contain any chapters examining the cognitive abilities of animals in the wild. It did, however, contain descriptions of work on wild animals trained and tested under laboratory conditions and seemed to herald a major expansion of work on comparative cognition to encompass a much wider range of species than previously tested. A decade and a half later, however, it is not clear that that promise is being realised. For example, food storing, once a model for

examining questions of the evolution of cognition and possibly the wildest of all the examples discussed in Balda et al. (1998), is now much less of a focus (e.g., Biegler, McGregor, Krebs, & Healy, 2001; Hampton & Shettleworth, 1996; Sherry & Vaccarino, 1989; but see Feeney, Roberts, & Sherry, 2009; Freas, LaDage,

Acknowledgements: We thank Rachael Marshall for helpful comments on an earlier version of manuscript, NSERC for funding T.A.H. and all of the cabin team for their contributions to this work. Corresponding author: susan.healy@st-andrews.ac.uk All previously published figures and photographs are used with permission of the authors.

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Roth, & Pravosudov, 2012). Food storing did, however, lead to perhaps the greatest recent flurry of excitement and effort in comparative cognition (Clayton & Dickinson, 1999): the examination of cognitive abilities in corvids. Subsequent work is now ranging from examination of episodic-like memory in a number of species including rats (Babb & Crystal, 2005), magpies *Pica pica* (Zinkivskay, Nazir, & Smulders, 2009), chickadees *Poecile atricapillus* (Feeney, et al., 2009), hummingbirds (Henderson, Hurly, Bateson, & Healy, 2006a), and meadow voles *Microtus pennsylvanicus* (Ferkin, Combs, Delbarco-Trillo, Pierce, & Franklin, 2008) to examination of problem-solving in a variety of contexts, typically by corvids but not always (Auersperg, Huber, & Gajdon, 2011; Dally, Emery, & Clayton, 2010; Schmidt, Scheid, Kotrschal, Bugnyar, & Schloegl, 2011; Taylor, Elliffe, Hunt, & Gray, 2010; Teschke & Tebbich, 2011; Weir, Chappell, & Kacelnik, 2009).

In fact, much of comparative cognition can be comfortably addressed in the laboratory, even when wild animals are tested. This may help to explain why there continues to be very little examination of cognitive abilities of animals in the wild, in what might be considered to be the real world. That world is one in which animals are faced daily with getting food, finding mates, avoiding predation, and this is where selection acts on cognitive abilities, perhaps favouring animals that are generally smart or, alternatively, favouring animals that are good at solving particular problems. The questions, then, differ slightly from those asked of animals in a laboratory i.e., not just what animals can do but what and how do they put those abilities to work when the test itself does not occupy much of their day. It is possible that we will find that animals' cognitive abilities in the field differ little or not at all from those we see in the laboratory. For example, the use of food deprivation in the laboratory to motivate animals to perform a test may resemble the state in which many wild animals find themselves i.e., often hungry and very willing to work for reliable food rewards. On the other hand, having to watch out for predators or competitors



Figure 1. A photo showing the landscape in which we train and test our hummingbirds. Birds typically defend territories that contain both open fields and some wooded areas. In this photo, one bird defended a territory at the far end of the field and a second male defended a territory around the location at which the photograph was taken. Photo by T. A. Hurly.

may mean that animals attend to experimental features differently than if they were to be tested in the field or the spatial scale over which testing occurs (Figure 1). Natural conditions might also lead to different cue use or different cue weighting than we see when animals are tested in boxes, arenas or (relatively) small rooms in the laboratory.

Going out into the field to test cognitive abilities certainly shares problems with laboratory tests, not least of which is being sure that the animal 'answers' the question experimenters think they are asking. If an animal fails to respond in an experiment, for example, it is frequently unclear whether this is because the animal is not motivated to respond or does not 'know' how to respond. Only when the animal does make a response that seems vaguely appropriate can we begin to measure its performance. Even then, variation in its performance may be due to motivation rather than to cognitive ability per se. In the field the animal may be distracted mid-test or simply fail to return to the test after failing to find a reward. A second major issue that has arisen with recent tests of cognitive ability in the wild is with the 'unit of measurement' for cognitive ability, especially when problem solving is that measure. Thus far, we are

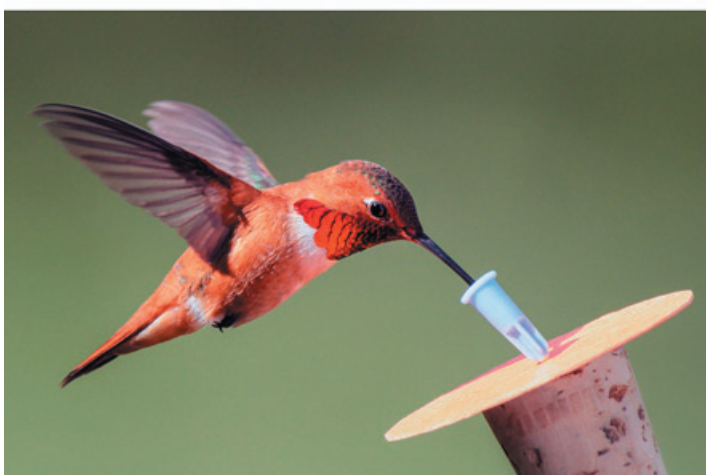
COMPARATIVE COGNITION & BEHAVIOR REVIEWS

not aware of a general consensus as to what constitutes a problem or what makes one problem more difficult than another. For example, currently, manipulation of physical material to retrieve food from manmade devices is considered by some to require ‘complex’ cognition although an apparently similar manipulation of materials to build a nest, however complex, is not (Seed & Byrne, 2010; but see Muth & Healy, 2011; Walsh, Hansell, & Healy, 2010; Walsh, Hansell, Borello, & Healy, 2011; van Casteren, Sellers, Thorpe, Coward, Crompton, Myatt, & Ennos, 2012). Is a problem considered more difficult if it has more steps to the solution, even if each

step is ‘easy’, or is a problem more difficult if it is more novel, either in appearance or in its solution? It would seem that there is a problem in using problem solving as a measure for cognitive abilities in animals. And if we have no measure that is readily quantifiable, then it will not be possible determine the causes or consequences of variation in that measure, within or across species.

It will come as no surprise that we have not attempted to examine problem solving in our work examining the cognitive abilities of rufous hummingbirds, trained and tested in the wild at our

Figure 2. Four examples of the kind of feeding device to which the birds can be readily trained. With these ‘flowers’ we can vary the quantity of sucrose, the number of flowers, their spatial proximity and their visual features. The photograph at the top left is of a board of the kind we use in the context-dependent experiments. The next two photographs show birds about to and feeding from our most commonly-used flower type, a cardboard disc with a central well formed from a syringe tip or cap. The bottom right photograph shows a hummingbird choosing florets on artificial inflorescences. Photos by T. A. Hurly.



COMPARATIVE COGNITION & BEHAVIOR REVIEWS

field site in the eastern Rocky Mountains, Alberta, Canada. At least, we have not looked at their ability to manipulate tools or to solve problems of the kinds that crows and others are now being set. Rather we have required ourbirds to learn to feed from all manner of devices (Figure 2), which they have invariably been very quick to do, typically learning within a couple of hours where to insert their tongue to receive sugar solution (sucrose). Although some might say that speed of learning in itself indicates cognitive ability (e.g., Boogert, Fawcett, & Lefebvre, 2011; Keagy, Savard, & Borgia, 2012), the fact that these birds learn so readily has for us largely meant that they are a useful species for examining cognition in the field: animals that took

100's or 1000's of trials to learn how to solve a task would have led us to look for other species. Here we review our work with two aims in mind: (1) to show that basing an experimental framework on knowing the ecology of a species can lead to a useful understanding of that species' cognitive abilities, and, (2) in light of the paucity of work done in the wild, we want to use our work on rufous hummingbirds as a case study to show what is possible to do in the messiness of the field, where our control over the animal's behaviour and experience is compromised. We would hope to show that such a pursuit can be both fruitful and that by doing so we add usefully to our understanding of cognition acquired from laboratory experiments. By so doing we

Figure 3. Photographs showing the elevated feeder (to deter bears) being lowered during pre-training (left), a newly marked bird in the hand (top right) and a marked bird feeding during an experiment (bottom right). Photos by T. A. Hurly.



COMPARATIVE COGNITION & BEHAVIOR REVIEWS



Figure 4. Once they arrive at our field site, the males establish feeding territories centred around feeders we have hung along the valley a week or two before they arrive. Typically the feeders contain 14% sucrose, which is much weaker than the nectar provided by the flowers from which the birds would normally feed. Photo by T. A Hurly.

would hope to encourage others similarly to go out into the field to examine cognition in other species. If we want to understand the evolution of cognitive abilities, especially in the vertebrates, the answers will not come from work on a single species, irrespective of the depth of enquiry.

Interested as we are in comparative cognition, we have two significant reasons for attempting to determine

the cognitive abilities in a single species, specifically rufous hummingbirds, in the wild. Firstly, these birds are logistically amenable to testing. As described elsewhere (e.g., Healy & Hurly, 2003, 2004), the males (the focus of our efforts) are strongly territorial, excluding conspecifics from feeding and thus from being trained to use our experimental equipment, they can be readily marked for individual identification and they feed every 10-15 minutes throughout the day for the duration of the

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

breeding season (Figure 3). Although one might say that cognition is studied in the laboratory for logistic reasons such as experimental and experiential control, the choice of a species to test in the wild is, at this relatively early stage of such work, crucial to success. For example, the fact that our hummingbirds feed every 10-15 minutes means that we can collect a useful amount of data within a day and across our six-week field season. Choosing to work with animals that feed once a day or less often, would lead to major issues with training animals and collecting enough data, without each study taking a lifetime!

Equally key to the success of the endeavour is that the behaviour and ecology of these birds is such that we can readily formulate predictions as to the nature of the birds' cognitive abilities from our observations of the birds' foraging behaviour. Rather than using a rather arbitrary task to examine their cognitive abilities, we can attempt to test those abilities we would expect might have been favoured in these particular animals. Foraging behaviour in the male rufous hummingbirds, at least, typically consists of a male flying approximately every 10 minutes from a conspicuous perch in his territory to feed (from flowers or our feeders; Figure 4) for a handful of seconds before returning to his perch. The intervening time before his next foraging bout can be filled with a considerable activity as he is constantly on the lookout for conspecific males and females. Territorial males display to conspecific rivals by the flashing of their bright orange gorget (throat) feathers. If this does not deter an intruder, it will be chased off at high speed. Females are also chased, especially off the feeders, but they tend to move to a position near the ground while the male performs several display flights. These consist of the male flying up (some 15m) and then flying steeply downwards before pulling out of his dive just above the head of the female, flying a short upward sweep and ending with a waggle (a short series of oscillations in the vertical plane). He then either repeats this manoeuvre several times or flies to the female and performs a shuttle-flight - a series of short zig-zag buzzing flights

in front of her. The aim of this game is to persuade the female to mate (Hurly, Scott, & Healy, 2001). Although we have not measured the energy expenditure of the males' various flight acrobatics, it appears that they would be energetically expensive (Clark, 2009). Indeed, males tend to visit the feeder (flowers) within a few minutes of such displays, although their visits are still no longer than a few seconds. Our very first speculation with regard to their cognitive abilities, then, was that this small (about 3g) nectarivore, defending several hundred (or more) flowers and feeding about every ten minutes for a few seconds only, might benefit from remembering which flowers he had recently visited (Healy & Hurly 2001). Not only would he save time and energy by remembering where they were, it should be useful to remember whether he had emptied the flower(s), or not. A bird that could do this would return to territory defence and mate attraction more quickly having expended less energy.

The success of our very first, speculative experiment set the scene for most of the experiments that have followed. In that first experiment, we presented rufous hummingbirds with an open-field analogue of a radial-arm maze: an array of artificial flowers, some of which contained a small amount of sucrose solution (Healy & Hurly, 1995). The flowers were coloured cardboard discs approximately 6cm in diameter, each glued to the end of a wooden stake 60cm tall (Figures 2 and 5). They were arranged in a rough circle with about 70cm between neighbouring flowers. For this experiment, the flowers held 40µl, an amount that meant the birds should visit and drink all of the contents of about four of the eight flowers. We presented the birds with two versions of this delayed-non-matching-to-sample task: in one version, all eight flowers contained reward but we allowed birds to visit only up to four flowers on their first visit to the array and in the second version, all eight stakes were presented but only four bore flowers. For both versions, then, birds visited and emptied up to four flowers of their contents. On their return to the array, after intervals ranging from five minutes up to an

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

hour, all eight flowers were present but only the flowers that had not been visited in the first phase of the trial contained food. As predicted, the birds were much more likely to visit flowers they had not recently emptied. A follow-up experiment showed that birds were also more likely to visit the flowers that had been present when they first visited the array but from which they did not drink (Hurly, 1996; see also Henderson, Hurly, & Healy, 2001). Although memory for perhaps as many eight flowers is not in the ballpark of the number of flowers thought to make up the territory of these birds (perhaps a couple of thousand), the birds could remember not just where the flowers were but that they had emptied them.

That the birds could remember something about a flower's contents was confirmed by an experiment in which we were actually aiming to address the role that flower colour played in the birds' ability to learn which flowers to visit. We expected that the birds would pay attention to the colour of the flowers both because, like us, birds have well-developed colour vision and there is much anecdotal evidence that hummingbirds are attracted to red objects. There was also speculation that this predilection for red had led to the propensity for the Californian flora, which lie on the migratory path of these birds, to produce red flowers. In that experiment we presented the birds with four, individually coloured flowers, only one of which contained sucrose solution and too much for a bird to consume in one visit. Once a bird had found the rewarded flower and then left after drinking as much as he wished, we emptied the flower and switched it with one of the other flowers in the array. When the bird returned, he was more likely to go to the flower that was in the location of the flower he had most recently fed from, rather than to the flower with the colour of the earlier, rewarded flower (Hurly & Healy, 1996; Miller & Miller, 1971; Miller, Tamm, Sutherland, & Gass, 1985). Consideration of the nature of the birds' ecology helps to explain why these birds seemed to ignore the colour cue provided by the flower: in a field of flowers of the same species, colour does not help the bird determine which flowers will be rewarding. Colour



Figure 5. Flowers in an array used by Rachael Marshall (in photo) in one of her timing experiments, showing the proximity of the experimenter to the array. Photo by T. A. Hurly.

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

might, however, be used to find flowers in unfamiliar places, such as along a migratory route and red may well be more conspicuous against a background of browns and greens that make up a western North American mountain range. It has also been argued elsewhere that the ubiquity of red flowers along the migration route of the rufous has less to do with attracting hummingbirds than making flowers inconspicuous to insects, whose vision is poorer at longer wavelengths (Altshuler, 2003; Briscoe & Chittka, 2001; Raven, 1972).

The longer we have experimented with these birds, the more we have found evidence for their ability to learn information as is necessary, because we have found they will learn and remember the colours of flowers, we just had to ask them in the appropriate fashion. Two examples will illustrate this. Firstly, in an experiment in which we were primarily interested in the accuracy with which they could remember a location, some birds were trained that yellow flowers were rewarded while others were taught that red flowers were rewarded. This colour-reward association was learned within 2-3 experiences (Hurly & Healy, 1996). Secondly, we trained birds that three of the flowers in an array of ten contained sucrose solution. All of the flowers differed in their colour pattern. Once the birds had learned which were the rewarded flowers we moved the array 2m from the site of the original array so the birds could not use the location of the flowers to determine which were the rewarded flowers. However, it was not until we had also changed the shape of the moved array that we found that the birds had remembered the colours of the flowers rewarded in the first array (Hurly & Healy, 2002; Figure 6). The birds can and will learn and remember colour but our ability to demonstrate that they can and will do so required us to be much more particular about our experimental designs. We would have been both remiss and incorrect if we had concluded that rufous hummingbirds were unable to learn colour cues, a very ubiquitous cognitive ability.

Not only do we have to be particular about our experimental designs, we also have to be careful about

our expectations of what these birds may or may not be capable. Expectations of animals' cognitive abilities tend to come from two sources, some based on knowledge of the animals' ecology and others from what might loosely be described as being based on their brain size. Rufous hummingbirds weigh around 3g and, although they have a brain that is larger than expected for their body size (Ward, Day, Wilkening, Wylie, Saucier, & Iwaniuk, 2012), that brain is still not very large. Knowledge of the birds' ecology leads to expectations that these birds might, for example, pay more attention to spatial information than to colour information (but that they would still pay attention to colour in the relevant contexts), while their brain size might lead to expectations of noticeable limits to the capacity for and speed and the accuracy with which the birds learn spatial locations. We are familiar with onetrial learning from the retrieval successes of food-storers and from long-delay taste aversion learning but even in tasks where animals are highly motivated to learn locations such as in rats searching for hidden platforms in the Morris water maze, animals often either take several trials to learn a location or require some time exploring the location in a first visit. Like food-storing birds, rufous hummingbirds, however, learn the three-dimensional location of a reward from a single visit that lasts only a few seconds. They can return to that location even in the absence of the flower (Flores Abreu, Hurly, & Healy, 2012) and they can visit several such 'empty' locations. Usefully, hummingbirds can demonstrate their memory for a rewarding location in the absence of the local cues of that reward because they will fly to, and then hover at, that location, much as a rat in a water maze will swim back and forth over the place it has learned to find a hidden platform.

Although we have not measured the accuracy with which the birds can return to a flower that has been removed after a single visit, we have attempted to measure the 3-D accuracy of memories for a familiar location. We trained birds to fly to a rewarded flower (a red 8cm³ cardboard cube) in a large featureless field,

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

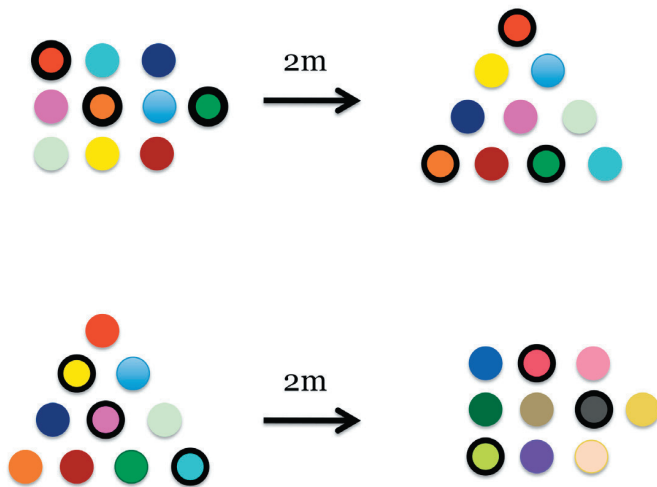


Figure 6. Schematic of the arrays used to determine that the birds did learn and remember colour (redrawn from Healy and Hurly 2002, above – treatment; below – control).

then removed the flower and filmed the bird's flight path into the location of the now-missing flower. The birds flew to within 60cm in the horizontal plane and within 20cm in the vertical plane (Hurly, Franz, & Healy, 2010). They did not appear to beacon to the flower in spite of the 'flower' being highly conspicuous, as when we simply moved the flower about 1.5m, the birds flew nearer to the location of the missing flower, and hovered, before flying directly to the moved flower. The birds' accuracy for a flower's location seems to depend on the size of the flower. In a second experiment, we trained birds to feed from either a small (8cm³) or a large flower (1000cm³). This time, in the absence of the flower, the birds flew even closer to its previous location than they had in the earlier experiment (the locations were not the same in the two presentations): 20cm in the horizontal and around 5cm in the vertical when the flower was small and around 50cm in the horizontal and about 25cm in the vertical when the flower was large. These data finally allowed us to confirm the precision with which a hummingbird can return to a learned but absent reward described in the many anecdotes of hummingbirds returning to sites of feeders they had fed from during their last migration or breeding season. The appearance of birds at particular windows of houses is a common

incentive for people to get feeders out of the cupboard after the winter.

One obvious difference for the birds in our experiments from the birds in these reports, however, was that we deliberately chose to place the experimental flower at least 10m from any obvious landmarks (e.g., bushes, trees; Figures 1 and 5). The data from experiments on various species in the laboratory would suggest that the birds might have learned the flower's location in one of three ways: they may have learned the visual characteristics of the flower and used it as a beacon, they could have used the landmarks proximal to the flower or, they used a number of distal landmarks. The behaviour of our real-world animals, however, does not readily conform to any of these three possibilities: while they can use the flower as a beacon, as shown by the birds flying to the moved flower once they discover the one in the familiar location is missing, they do not need to beacon to the flower and they do not do so preferentially. Graham, Fauria, & Collett, (2003) suggested that their ants might use large landmarks along a route as beacons while learning that route and that those landmarks might act as a scaffold for learning other landmarks nearby so that the animals could move along the route if the beacons were then removed. While this seems plausible for our hummingbirds it is not at all clear which landmarks along the way would have formed this scaffold. The proximal landmarks were (to our eyes, at least) remarkably uniform: the ground was quite flat, and covered by vegetation that reached perhaps 20cm punctured by multiple ground squirrel burrows. The distal landmarks, on the other hand, were very conspicuous and ranged from trees, typically ringing the open fields used for training and testing, to the mountains rising some 1000m along both sides of the valley and visible from all points in the open fields. However, it was still not clear how such large landmarks would enable the birds to be quite so accurate in their return to the flower location. It is possible that the birds did not use visual cues at all as they may well have used magnetic or sun compass cues instead but there is